Community Ecology 19(3): 239-247, 2018
1585-8553 © The Author(s).
This article is published with Open Access at www.akademiai.com
DOI: 10.1556/168.2018.19.3.5

Importance of thermophilous habitats for protection of wild bees (Apiformes)

J. Banaszak[1] and L. Twerd[1,2]

[1]*Kazimierz Wielki University, Institute of Environmental Biology, Department of Ecology, Ossolińskich 12, 85-093 Bydgoszcz, Poland*
[2]*Corresponding author: l.twerd@ukw.edu.pl*

Keywords: Natura 2000, Oder Valley, Poland, Sandy grasslands, Xerothermic grasslands.

Abstract: Research on wild bees (Apiformes) was conducted in the Lower Oder Valley (NW Poland) at Natura 2000 sites near the border between Poland and Germany. The analysis involved 3 landscape types with xerothermic and sandy grasslands, differing in the proportion of woody vegetation. In total, we collected there 4158 specimens of Apiformes, representing 180 species. We have proved that mid-forest grasslands with a high proportion of thermophilous broad-leaved forests and xerothermic shrub communities are equally attractive to wild bees as open habitats (sandy grasslands, xerothermic grasslands/heaths). We observed varied responses of wild bee species with specific functional characteristics to increasing proportion of woody vegetation. The grasslands surrounded by forests were characterized by the highest number of cleptoparasitic species. In contrast, solitary and social bee species preferred forest-steppe habitats. However, in open habitats, solitary bees were the most abundant. Moreover, open habitats were distinguished by the highest number and abundance of rare species. Active protection of thermophilous grasslands is crucial for biodiversity conservation, also with respect to the natural resources of Apiformes. Preservation of biodiversity in threatened xerothermic and sandy grasslands should be one of the key objectives of nature conservation in European countries. Currently, more and more actions are undertaken to improve their condition and to restore those particularly valuable and threatened habitat types.

Abbreviations: CCA–Canonical Correspondence Analysis; CVA–Canonical Variates Analysis; DCA–Detrended Correspondence Analysis.

Nomenclature: Michener (2007).

Introduction

According to many documented sources, the species richness and abundance of wild bees have decreased in Europe recently (Steffan-Dewenter and Tscharntke 2001, Biesmeijer et al. 2006, Carvell et al. 2006, Goulson 2006, Fitzpatrick et al. 2007, IPBES 2016). This may have serious ecological and economic consequences (Pywell et al. 2006, Potts et al. 2016). The changes in fauna observed on a global scale are associated mostly with the loss of natural and semi-natural habitats, and excessive fragmentation of landscape (Tscharntke et al. 2005, Murray et al. 2009, Ollerton 2017).

An important factor modifying the resources of Apiformes is also the natural plant succession, which in temperate climate leads to formation of shrub communities, followed by forests (Bornkamm 2006). Forest communities of the temperate zone are characterized by a lower diversity of bees than open habitats with good light conditions (Banaszak and Jaroszewicz 2009, Banaszak et al. 2009, Banaszak and Ratyńska 2014). Similarly, forest communities at the early stages of ecological succession can be richer in bee species than older forest stands (Taki et al. 2013).

Some of the rarest habitats, most threatened by secondary succession (Bakker and Berendse 1999, Pärtel et al. 2005) in western and central Europe, are semi-natural xerothermic and sandy grasslands. Preservation of these unique ecosystems is important for the European Union (Council Directive 92/43/EEC). In the currently dominating agricultural landscape in most of European countries, they are important components of local biodiversity and play the role of refugia for many groups of organisms (Cremene et al. 2005, Pykälä et al. 2005, Öckinger et al. 2006, Chmura et al. 2013, Fartmann et al. 2012).

Their uniqueness is linked with the specific combination of geological, spatial, and microclimatic conditions where these habitats are found. They support large and species-rich communities of Apiformes, and enable survival of species with distinct ecological requirements. Another factor modifying the resources of wild bees is also their provision with a rich and diverse food base (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Albrecht et al. 2010). This is particularly important in the context of successional transformations of grasslands, observed in the last 25 years in Europe. The changes are undoubtedly caused and intensified e.g., by discontinuation of grazing and extensive meadow management (Bornkamm 2006).

The deteriorating condition of xerothermic grasslands in European countries since the last century and their insuffi-

cient protection forced the member states of the EU to undertake activities leading to proper management of thermophilous grasslands. Many initiatives in Europe (e.g., research projects: "Conservation and development of the steppe grasslands in Thuringia" in 2009-2015; "Protection of xerothermic grasslands in Poland – theory and application" LIFE08 NAT/LP/513) are aimed to restore degraded grasslands and manage thermophilous habitats properly, as their preservation is important for protection of many groups of species, including the Apiformes.

Consequently, the goals of this study were: (1) to determine the role of distinguished thermophilous habitats in protection of the diversity; (2) to investigate the response of wild bees to increasing proportion of forest vegetation; and (3) to suggest how such habitats should be managed, particularly in the context of occurrence of species with distinct ecological requirements.

Material and methods

Study area

Research on wild bees (Apiformes) was conducted in the Lower Oder Valley, within the Cedynia Landscape Park (NW Poland). The explored sites are protected within the Natura 2000 network (Special Protection Areas and Special Areas of Conservation). The study sites are at the edge zone of the valley of the river Oder (Odra) between the villages of Osinów Dolny and Krajnik Dolny (Fig. 1).

For this study, we selected 7 sites with thermophilous vegetation (typical of xerothermic or sandy grasslands), which were divided into 3 landscape types: [A] open habitats: 1, 2, 4 (forest < 40% of the area, herbaceous vegetation >60% of the area, bare soil > 10% of the area); [B] forest-steppe habitats: 5, 7 (forest 40-60% of the area, herbaceous vegetation 60-40% of the area, bare soil < 10% of the area); [C] grassland surrounded by forest 3, 6 (forest > 70% of the area, herbaceous vegetation <30% of the area, bare soil < 5% of the area) (Fig. 1). To avoid spatial autocorrelation, all the sites were at least 1.5 km apart.

Six of the 7 sites were sampled in 2014 and 2015 whereas one site was observed in 2012 and 2013. We explored the following sites: [1] "Wrzosowiska Cedyńskie" nature reserve, near Osinów Dolny in 2014 and 2015; [2] Cedynia in 2014 and 2015; [3] "Bielinek" nature reserve, near Markocin in 2012 and 2013; [4] Piasek in 2014 and 2015; [5] "Słoneczne Wzgórza" nature reserve near Raduń in 2014 and 2015; [6] Zatoń in 2014 and 2015; and [7] Krajnik Dolny in 2014 and 2015 (Table S1, Fig. 1). In this area slopes covered by xerothermic vegetation reach up to 60–80 m a.s.l. The types of vegetation and proportions of thermophilous forest and shrub communities, xerothermic grasslands, and other types of vegetation attractive to bees found at individual sites are presented in Table S1.

The landscape of the study area is characterized by high, wooded moraines and sandurs. The floodplain in the river valley is dominated by wetlands. In contrast, on slopes and other sites that are not flooded, dry grassland ecosystems have developed (including xerothermic grasslands), with unique species of thermophilous and steppe plants, such as *Quercus*

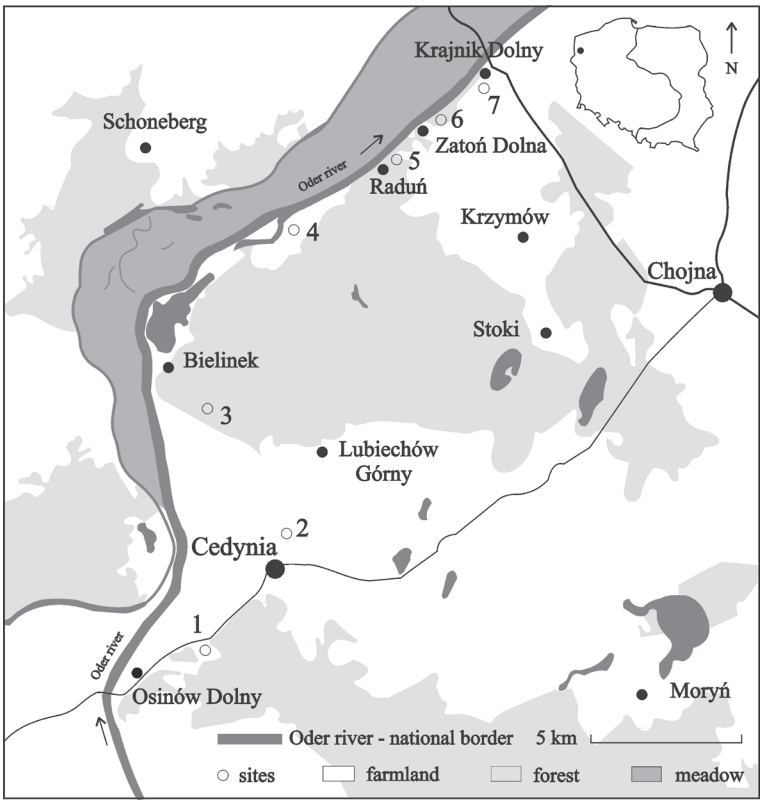

Figure 1. Study sites with thermophilous vegetation (xerothermic and sandy) located in the Lower Oder Valley between the villages of Osinów Dolny and Krajnik Dolny. 1 = "Wrzosowiska Cedyńskie" nature reserve; 2 = Cedynia; 3 = "Bielinek" nature reserve; 4 = Piasek; 5 = "Słoneczne Wzgórza" nature reserve; 6 = Zatoń; 7 = Krajnik Dolny.

pubescens Willd., *Prunus fruticosa* Pall., *Lithospermum purpurocaeruleum* L., *Dorycnium herbaceum* Vill., *Inula germanica* L., *Stipa joannis* Čelak, *Stipa pulcherrima* K. Koch, *Stipa capillata* L., *Anthericum liliago* L., *Galatella linosyris* (L.) Rchb.f., *Hieracium echioides* Lumn., *Oxytropis pilosa* DC., *Scabiosa canescens* Waldst. & Kit., *Campanula bononiensis* L., *Campanula sibirica* L., *Scorzonera purpurea* L., *Medicago minima* (L.) Bartal. or *Salvia pratensis* L. Simultaneously, west of the edge zone of the valley, extensive forests prevail, while farmland covers much smaller areas.

Insect sampling

Field research was conducted in 2012-2015 from May till August. At all the study sites we took quantitative samples using the transect method (transects 200 m long and 1 m wide) in conditions favourable for bee activity, i.e., with no or very little wind, at temperatures in summer exceeding 20˚C (Banaszak 1980). As a rule, in the first year of investigations at a given site we collected samples in summer (June and July or early August), and in the second year in spring (May), after the detailed field research. (Thus we carried out field research in summer in 2012, spring in 2013, summer in 2014, and spring in 2015.) At each site, samples were collected within a radius of 250 m from the center of the study sites. Sample collection along each transect lasted about 30 min. We assumed the necessity of making the catches within 6 dates (2 dates in spring, 4 dates in summer) and crossing each time 3 transects – 1.5 h in a given site. But in fact, in some cases, we modified this assumption due to difficult terrain (e.g., large differences in relative altitude, very steep slopes, landslides – which resulted in increased time to cross and the same in increased number of transects). On the other hand, the number of dates may have been modified due to unstable weather conditions.

In total, 135 samples were taken: Sites: [1] 3 dates × 7 transects; [2] 4 dates × 3 transects; [3] 6 dates × 5 transects; [4] 4 dates × 3 transects; [5] 6 dates × 5 transects; [6] 5 dates × 3 transects; [7] 5 dates × 3 transects.

Names of species and information on functional characteristics of species follow Michener (2007). We analysed the occurrence of species in respect of nesting sites (soil, cavity, hive), social behaviour (solitary, eusocial, cleptoparasite), and threat category in Poland (rare, common). We classified as rare all the species that were assigned a threat category by Bogdanowicz et al. (2004) (Table S2).

Within nature reserves, research was conducted with permission of the Regional Director of Environmental Protection in Szczecin (Decision no. 27/2013; WOPN-ON.6205.15.2015.AR).

Habitat characteristics

At each site we determined parameters describing landscape structure (proportions of forest and shrub communities, thermophilous forest and shrub communities, herbaceous vegetation, bare soil, and habitat heterogeneity). We assessed landscape structure within the radius of 250 m, i.e., around the sites where insects were caught. The analysis was based on topographic maps on a scale of 1:2000, by using ArcGis software and direct field research. A measure of habitat heterogeneity (H) was the Shannon index of diversity:

$$H = -\sum_{i=1}^{N} n_i \left(\log_2 n_i\right) \ ,$$

where H is heterogeneity, n_i is the area of individual types of vegetation, and N is the total investigated area.

Heterogeneity was determined on the basis of percentage contributions of forest and shrub communities, thermophilous forest and shrub communities (jointly for each category), herbaceous vegetation, and bare soil, within the designated area.

The list of thermophilous forest and shrub communities is presented in Table S1. The other forest communities were dominated mostly by *Pinus sylvestris* and *Betula pendula*.

Statistical analysis

The observed species richness was assessed using rarefaction curves (Gotelli and Colwell 2001). The computations were performed with EstimateS software (Colwell 2006). The extrapolated species richness (the number of observed species and the unobserved ones) was estimated using Chao1 estimator (Chao 1984).

Numerical analysis of the collected data was performed using CANOCO v. 4 software (ter Braak and Šmilauer 1998). To detect a gradient in total variation of the data, we performed detrended correspondence analysis (DCA). The gradient was 3.41 standard deviations long, so in further calculations we used unimodal methods (ter Braak and Šmilauer 1998). Data on species were transformed logarithmically [log(x)]. We excluded from the model the species that were represented by single specimens.

By using canonical correspondence analysis (CCA), we determined the influence of variables describing landscape structure (see Material and Methods, Habitat characteristics) on occurrence of individual species of Apiformes. The site and year = phenological period we also used as conditional factors.

To accunt for spatial and temporal correlations among collected data, linear mixed models were used. Year and site were considered random effects and landscape type was considered fixed effect. P-values were calculated using Wald's method. Calculations were done in R package with lme4 library (Bates et al. 2015, R Core Team 2017).

The last stage of the analyses was aimed to determine the importance of functional groups of wild bees and identify which of the analysed features differentiates most strongly the studied set of species in the 3 compared landscape types. For this purpose, we used canonical variates analysis (CVA). The species for which a given functional feature was not determined were excluded from analysis.

To assess the significance of the tested variables and canonical axes, we performed a Monte Carlo permutation test with 1000 repeats. We assessed the influence of only statistically significant variables ($p < 0.05$).

Results

Taxonomic composition of bee communities

In total, we recorded 180 species of wild bees (Hymenoptera: Apiformes) of 33 genera, represented by 4158 individuals (Table S2). They account for 37% of all bee species reported from Poland. The most numerously represented genera were: *Andrena* (31 species), *Lasioglossum* (21 species), *Bombus* (18 species), *Nomada*, and *Sphecodes* (15 species each).

About 12% of the recorded bee species are rare or threatened in Poland (Table S2). Some of the recorded species are included in the European Red List of Bees. One of them is endangered (EN), 2 are vulnerable (VU), 12 are near-threatened (NT), 28 are data deficient (DD), and 131 are of least concern (LC), so they jointly account for about 96% of the total number of recorded taxa.

In the analysed bee community, only 2 species were dominants (> 5%): *Lasioglossum calceatum* and *Lasioglossum morio* (Table S2). As many as 101 species (56.42%) were represented by > 5 individuals, 40 species by single specimens (22.09%), and 58 (32.04%) were recorded at only 1 locality (Table S2).

Table 1. Results of stepwise selection of variables and a Monte Carlo Permutation Test – analysis of the significance of the effect of studied variables on occurrence of different species of Apiformes; variables were significant at $p < 0.05$.

Variables	CCA		
	Level of significance	Variation	% of explained variation
habitat heterogeneity	0.007	0.23	19.33
thermophilous forest and shrub communities	0.002	0.22	18.87
bare soil	0.003	0.15	2.69
site	0.010	0.15	1.89
year = phenological period	0.020	0.12	1.81

Open habitats vs. forest-steppe habitats

We assessed the attractiveness of individual thermophilous habitats. The assessment was based on the observed number of recorded species and the estimates made using Chao1 estimator. Our results show that the most attractive to bees were forest-steppe habitats with xerothermic grasslands (sites 5, 7) as well as sites dominated by xerothermic and sandy grasslands (1, 2 and 4) (Table S2). In those 2 groups, the estimated number of bee species (those observed and possible do detect) was 165 and 149, respectively. The least attractive to bees were forest glades in forest-steppes (sites 3, 6). In that group, the estimated number of bee species (those observed and possible do detect) was only 129 (Table S2).

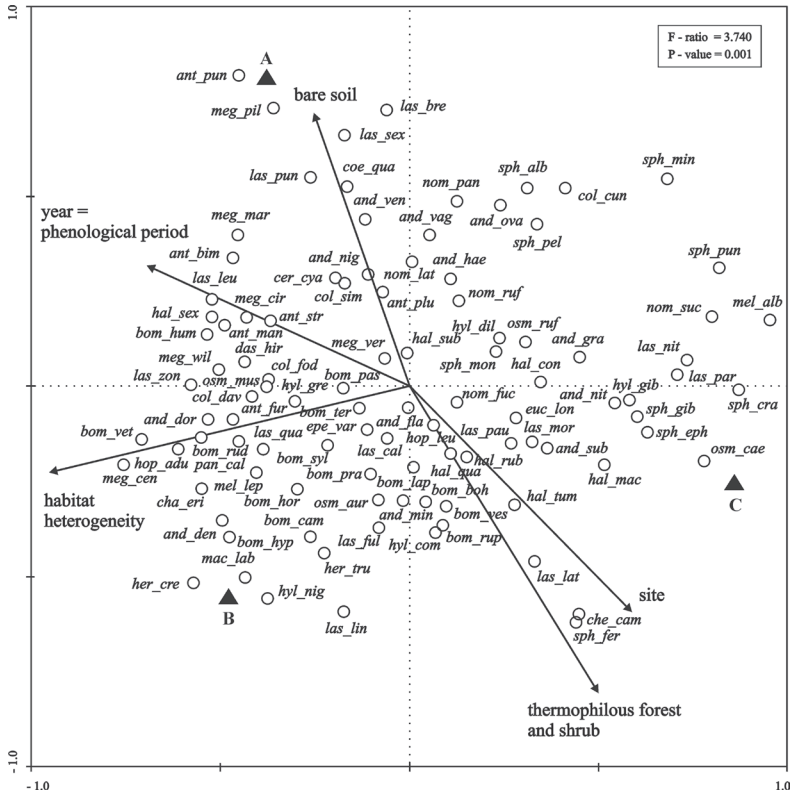

Figure 2. Ordination diagram based on canonical correspondence analysis (CCA), presenting the distribution of 101 species of Apiformes along axes I and II and vectors of the analysed variables. All variables used in the analysis explained significantly 51.59% of the variation in Apiformes species data (the sum of all canonical eigenvalues: 0.873, the sum of all eigenvalues: 1.692; 0.873/1.692=0.515 i.e., 51.59%). Legend for landscape types: A = open habitats; B = forest-steppe habitats; C grasslands surrounded by forests.

Table 2. Effects of landscape type on richness, abundance and diversity wild bees. The table shows results of linear mixed models taking into account spatial and temporal correlations among collected data; bold estimates indicate significant effects at $p < 0.05$.

Landscape type	Estimate ± SEM	z value	p
Richness			
forest-steppe vs. open habitats	**18.58 ± 9.86**	3.69	< 0.001
grasslands surrounded by forests vs. open habitats	14.08 ± 30.05	0.92	0.358
grasslands surrounded by forests vs. forest-steppe	-4.5 ± 30.37	-0.29	0.771
Abundance			
forest-steppe vs. open habitats	**169.17 ± 121.54**	2.73	0.006
grasslands surrounded by forests vs. open habitats	118.42 ± 337.42	0.69	0.492
grasslands surrounded by forests vs. forest-steppe	-50.75 ± 341.77	-0.29	0.771
Diversity			
forest-steppe vs. open habitats	**0.42 ± 0.38**	2.21	0.027
grasslands surrounded by forests vs. open habitats	0.37 ± 0.57	1.27	0.205
grasslands surrounded by forests vs. forest-steppe	-0.05 ± 0.6	-0.18	0.857

Effect of landscape structure on species occurrence

Our results show that 5 variables significantly affected the occurence of species (Table 1). The distribution of individual species in relation to analyzed variables is presented in Figure 2.

The structure of bee communities along the gradient of forest cover

We have demonstrated significant differences in the richness, abundance and diversity of bee species between forest-steppe habitats and open habitats. The values of the above indicators were significantly higher in forest-steppe habitats. At the same time, we have not found significant differences in the values of these indicators for grasslands surrounded by forests versus open habitats, or between habitats with a higher share of woodland, i.e., between forest-steppe and grasslands surrounded by forests (Table 2).

The highest number of species (127) were collected in forest-steppe habitats (B), which were the most heterogeneous. We also observed similar regularities with regard to the abundance and diversity of bees, as forest-steppe habitats (B) turned out to be the most attractive for bees (1536 individuals, diversity = 3.416) (Table S2).

Importance of functional groups and traits of Apiformes

Results of CVA show that with respect to species number, the analysed bee community significantly differed in proportions of cleptoparasitic, solitary, rare, common, and ground-nesting species (Table 3, Fig. 3). The largest number of cleptoparasitic species (32) was noted in grassland surrounded by forest (C). In contrast, in forest-steppe habitats (B), we recorded the largest numbers of species of solitary bees (77), common bees (121), and those nesting in the ground (63).

Table 3. Results of stepwise selection of variables and a Monte Carlo Permutation Test – analysis of species characteristics used in canonical variate analysis (CVA); marked variables were significant at $p < 0.05$.

Variables	CVA - richness		
functional group and traits	Level of significance	Variation	% of explained variation
cleptoparasite	0.001	0.24	7.94
rare	0.001	0.16	5.64
solitary	0.001	0.12	4.04
common	0.003	0.16	3.63
soil	0.037	0.09	3.24
Variables	CVA - abundance		
functional group and traits	Level of significance	Variation	% of explained variation
rare	0.001	0.24	5.25
solitary	0.009	0.23	4.68
eusocial	0.011	0.13	2.66
soil	0.038	0.10	2.31

Open habitats (A) were characterized by the highest number of rare species (11) (Table S2, 3, Fig. 3).

Results of CVA show that regarding abundance of the collected species, the analysed bee communities significantly differed in proportions of specimens of rare, solitary, social, and ground-nesting species (Table 3, Fig. 3). In forest-steppe habitats (B), the highest abundance was reached by solitary bees and those nesting in the ground (62 and 747 specimens, respectively). In contrast, open habitats (A) were characterized by the highest abundance of bee species that are solitary or rare in Poland (664 and 52 specimens, respectively) (Table S2, 3, Fig. 3).

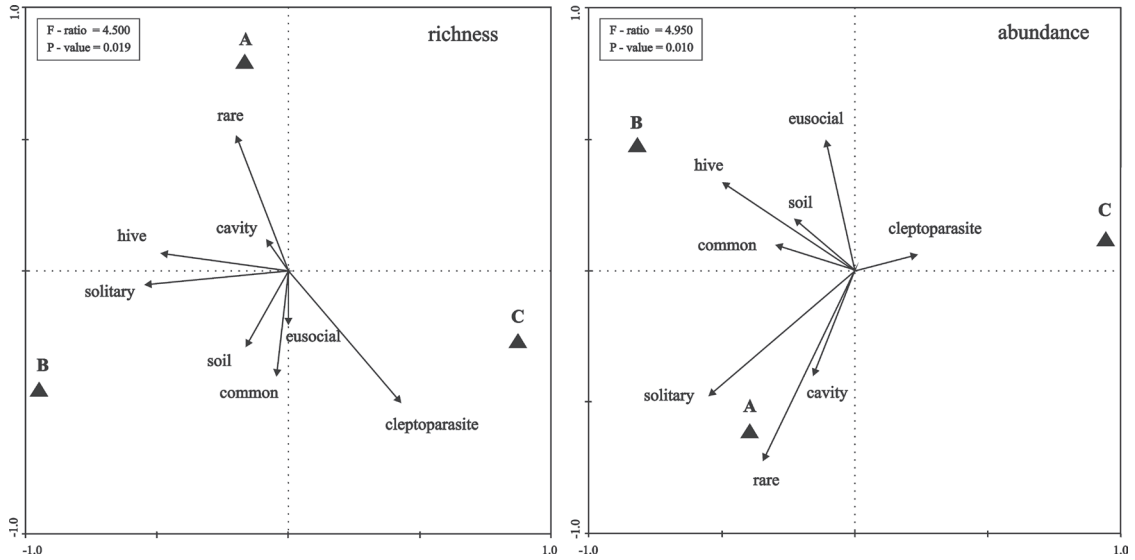

Figure 3. Ordination diagram based on canonical variates analysis (CVA) presenting the location of sites and vectors of variables. Functional traits: nesting sites (cavity, soil, hive) and social behaviour (solitary, eusocial, cleptoparasite); threat category (rare, common). Landscape types: A = open habitats; B = forest-steppe habitats; C = grasslands surrounded by forests.

Discussion

Preservation of biodiversity of thermophilous grasslands and their proper management are one of the priorities of EU member states. Unfortunately, however, the attention of decision-makers is focused on vegetation only. The success of protection measures is conditioned not only by protection of vegetation but also of various groups of animals, including wild bees, which are crucial for proper functioning of many ecosystems (Young 2000, Griffin et al. 2016).

In the study area, we recorded 180 species of wild bees. This is a high number, but not as high as in xerothermic habitats located in the Lower Vistula Valley, where as many as 253 bee species were found (Banaszak et al. 2006). This difference can be explained by the structure of land use in both regions. The areas along the Vistula are more populated and characterized by a much higher proportion of xerothermic grasslands, maintained by human activity. In contrast, the areas along the Oder, lying in the border zone, are markedly less strongly affected by human activity. That, is why in many cases, as a result of ecological succession, xerothermic communities were transformed there into forest communities. In spite of negative changes, they are still important habitats for wild bees. Their importance for protection of Apiformes can be confirmed e.g., by the high contribution of rare and threatened species to the total number of recorded taxa: 12% on the scale of Poland and 96% on the European scale (Bogdanowiocz et al. 2004, Nieto et al. 2014).

Patches of thermophilous vegetation in the Lower Oder Valley are relatively small, isolated. They are mostly located on steep slopes along the river, often in immediate vicinity of arable fields or hay meadows. That is why in this case landscape structure plays an important role in shaping the richness of Apiformes.

We assessed the attractiveness of individual thermophilous habitats. We found that grasslands surrounded by a high proportion of thermophilous broad-leaved forests and xerothermic shrub communities (B and C) are extremely attractive to wild bees. When analysing the changes in the structure of bee communities along the gradient of forest cover, we found that the diversity of Apiformes was comparable in open and forest-steppe habitats. The highest values of the analysed indices: number of species, abundance and diversity were recorded in forest-steppe habitats of type B, characterized by the highest structural and floristic variation of plant communities. Other researchers also reported that habitat heterogeneity is a significant factor determining the natural resources of Apiformes (Meyer et al. 2007, Diacon-Bolli et al. 2012). An important role is played also by landscape heterogeneity and presence of habitats attractive to wild bees (Svensson et al. 2000, Söderström et al. 2001, Steffan-Dewenter and Tscharntke 2000, 2001). Varied landscape increases the probability that within the flight distance of bees, all the environmental attributes necessary for them will be available, i.e., suitable sites for nesting, courtship flights, and foraging for food (Cierzniak 2003).

Succession is a factor determining both an increase and a decrease in habitat heterogeneity. All this results in the observed changes in the variation of species at the consecutive stages of succession (Banaszak and Ratyńska 2014). However, the patterns of successional transformations of vegetation and of communities of the associated pollinating insects may vary and depend e.g., on habitat type and quality, the possibility to colonize the habitat, and biotic interactions between organisms. They are also modified by the influence of other natural factors and human impact (Potts et al. 2003, Banaszak et al. 2017). However, irrespective of the factors affecting the rate of ecological succession, in temperate climate

it is always directed towards formation of forest communities (Faliński 1986, Prach 2003).

Thermophilous grasslands situated in the Lower Oder Valley and in other parts of Poland are examples of semi-natural ecosystems, which can be protected only actively, i.e., if livestock grazing or extensive meadow management is maintained. As an initiative associated with protection and proper management of grassland habitats, in 2010-2013 in the Lower Oder Valley the project "Protection of xerothermic grasslands in Poland – theory and application LIFE08 NAT/LP/513" was implemented (Barańska et al. 2013). Within the framework of that project, xerothermic flora and vegetation were surveyed and the major threats to their proper functioning were presented. Simultaneously, as part of the project, various activities were undertaken to restore some of the grasslands and to slow down the process of secondary succession (e.g., by cutting of trees and shrubs in "Słoneczne Wzgórza" nature reserve, systematic elimination of self-sown young trees and shrubs in grasslands, removal of sheep fleece, transportation of grazing sheep from one place to another) (Barańska et al. 2013). Similarly, in 2003-2006, on the initiative of Gaia Club members, trees and shrubs were cut in "Bielinek" nature reserve. This resulted in a mosaic of habitats: wooded (about 70%) and open (about 30%), so the living conditions for many species of plants and animals were greatly improved.

Results of the present study show that the attractiveness of open and forest-steppe habitats was comparable. Thus, we suppose that the results were strongly affected by management practices conducted a few years earlier in "Bielinek" nature reserve and, to a lesser extent, in "Słoneczne Wzgórza" nature reserve. Thanks to those management practices, patches of thermophilous vegetation attractive to wild bees were exposed. Also Yamaura et al. (2012) report that habitats resulting from forest management practices (e.g., pruning, thinning), generate more flower resources and thus are more attractive to the Apiformes. Moreover, results of other studies have indicated that bees can quickly colonize the available habitats (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Griffin et al. 2016), and the generated structure of the new bee community can be similar to that of undisturbed habitats (Forup and Memmott 2005, Forup et al. 2007, Hopwood 2008, Exeler et al. 2009, Tarrant et al. 2013). Simultaneously, some examples indicate both instability (Williams 2011) and stability during the richness of bees in restored habitats (Griffin et al. 2016). On the basis of our results we conclude that in some cases restored habitats are distinguished by exceptionally high species richness, abundance, and diversity of Apiformes, even 10 years after the management practices. Unfortunately, changes in the structure of wild bee communities in restored habitats are poorly studied, especially in the context of long-term research.

In our study we also attempted to answer the question: how do the functional groups respond to an increase in forest cover? In this context, we investigated changes in proportions of species with given functional features. We found that the number of species of cleptoparasitic bees was the highest in grassland surrounded by forest, i.e., the landscape type with the highest forest cover. This finding confirms that bee communities are stable in this habitats type. Undoubtedly, the occurrence of nest parasites and their high proportion in the bee community indicate that the populations of the host species are stable (Calabuig 2000). Moreover, cleptoparasitic bees, using the food resources of other species, are not so dependent on the richness of flowering plants, which e.g., in oak-hornbeam forests are abundant only in spring. Similar results, i.e., high contributions of cleptoparasitic species to bee communities in natural oak-hornbeam forests, were reported by Banaszak and Cierzniak (1994). We also found that the other functional groups of species, both solitary and social, preferred forest-steppe habitats, which were characterized by the most variable site conditions, enabling simultaneous occurrence of species with different ecological requirements. Besides, the relatively high contribution of grass-dominated communities with sparse vegetation in forest-steppe habitats enabled many bees to build nests in the ground. However, solitary bees were the most abundant in open habitats. This results from the dominance of *Colletes cunicularius* (2.9%), a species associated with sandy, sparsely vegetated sites. In those habitats we recorded also a high proportion of its nest parasite, *Sphecodes albilabris* (2.7%). Simultaneously, open habitats were characterized by the highest number and abundance of species that are rare in Poland. In most cases they were species noted only in open habitats, and their proportion declined with increasing forest cover.

Our results allow us to conclude that grassland habitats with a high proportion of thermophilous broad-leaved forests and xerothermic shrub communities in the vicinity are equally attractive to wild bees as open habitats. At the same time, our findings unambiguously attest to the high conservation value of these ecosystems. Their decline is linked with discontinuation of extensive meadow management and with ecological succession, leading to gradual colonization of grasslands. Undoubtedly, in respect of protection of thermophilous grasslands, the best form of land use is varied land use, consisting in creating a mosaic of habitats, both in time and space (Barańska et al. 2013). That is why proper management of grassland habitats should be based on active protection, entailing maintenance of the habitats at optimum stages of succession, taking into account the possibility to protect not only flora, but also various groups of animals.

References

Albrecht, M., M. Riesen and B. Schmid. 2010. Plant-pollinator network assembly along the chronosequence of a glacier foreland. *Oikos* 119:1610–1624.

Bakker, J.P. and F. Berendse. 1999. Constrains in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol*. 14:63–68.

Banaszak, J. 1980. Studies on methods of censusing the numbers of bees (Hymenoptera, Apoidea). *Polish Ecol. Stud.* 6(2):355–366.

Banaszak, J. and T. Cierzniak. 1994. Spatial and temporal differentiation of bees (Apoidea) in the forests of Wielkopolski National Park, Western Poland. *Acta Univ. Łodz., Folia zool*. 2:3–28.

Banaszak, J., T. Cierzniak, R. Kriger and J. Wendzonka. 2006. Bees of xerothermic swards in the lower Vistula valley: diversity and

zoogeographic analyses (Hymenoptera: Apoidea: Apiformes). *Polish J. Entomol.* 75:511–537.

Banaszak, J. and B. Jaroszewicz. 2009. Bees of the Białowieża National Park and adjacent areas, NE Poland (Hymenoptera: Apoidea, Apiformes). *Polish J. Entomol.* 78:281–313.

Banaszak, J., R. Kriger and T. Cierzniak. 2009. Bees (Hymenoptera: Apoidea, Apiformes) of the Drawa National Park. *Polish J. Entomol.* 78:135–156.

Banaszak, J. and H. Ratyńska. 2014. Local changes in communities of wild bees (Hymenoptera: Apoidea, Apiformes): 30 years later. *Polish J. Entomol.* 83:325–351.

Banaszak, J., L. Twerd, A. Sobieraj-Betlińska and B. Kilińska. 2017. The Moravian Gate as route of migration of thermophilous bee species to Poland: fact or myth? A case study in the "Góra Gipsowa" steppe reserve and other habitats near Kietrz. *Polish J. Entomol.* 86:141–164.

Barańska, K., M. Żmihorski and P. Pluciński. 2013. *Raport z projektu Ochrona muraw kserotermicznych w Polsce – teoria i praktyka LIFE08 NAT/PL/513*, Wydawnictwo Klubu Przyrodników, Świebodzin.

Bates, D., M. Maechler, B. Bolker and S. Walker 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67(1):1–48.

Biesmeijer, J.C., S.P.M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A.P. Schaffers, S.G. Potts, R. Kleukers, C.D. Thomas, J. Settele and W.E. Kunin. 2006. Parallel declines in pollinators and insect pollinated plants in Britain and the Netherlands. *Science* 313:351–354.

Bogdanowicz, W., E. Chudzicka, J. Pilipiuk and E. Skibińska. 2004. *Fauna Polski – charakterystyka i wykaz gatunków*, 1. Muzeum i Instytut Zoologii PAN, Warszawa.

Bornkamm, R. 2006. Fifty years vegetation development of a xerothermic calcareous grassland in Central Europe after heavy disturbance. *Flora* 201:249–267.

Carvell, C., D.B. Roy, S.M. Smart, R.F. Pywell, C.D. Preston and D. Goulson. 2006. Declines in forage availability for bumblebees at a national scale. *Biol. Conserv.* 132:481–489.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Stat.* 11:265–270.

Calabuig, I. 2000. Solitary bees and bumble bees in a Danish agricultural landscape. Ph.D.thesis. Dept. Popul. Ecol., Univ. Copenhagen.

Cierzniak, T. 2003. Ekologia pszczół w dynamicznym kręgu zbiorowisk grądowych. Wydawnictwo Akademii Bydgoskiej im. Kazimierza Wielkiego, Bydgoszcz.

Chmura, D., P. Adamski and Z. Denisiuk. 2013. How do plant communities and flower visitors relate? A case study of seminatural xerothermic grasslands. *Acta Soc. Bot. Pol*. 82(2):99–105.

Colwell, R.K. 2006. EstimateS: Statistical estimation of species richness and shared species from sample. Version 8.0.0. User's Guide and applications published at: http://purl.oclc.org/estimates.

Cremene, C., G. Groza, L. Rakosy, A.A. Schileyko, A. Baur, A. Erhardt, et al. 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conserv. Biol.* 19(5):1606–1618.

Diacon-Bolli, J., T. Dalang, R. Holderegger and M. Bürgi. 2012. Heterogeneity fosters biodiversity: Linking history and ecology of dry calcareous grasslands. *Basic Appl. Ecol.* 13:641–653.

Exeler, N., A. Kratochwil and A. Hochkirch. 2009. Restoration of riverine inland sand dune complexes: implications for the conservation of wild bees. *J. Appl. Ecol.* 46:1097–1105.

Faliński, J. 1986. Vegetation dynamics in temperate lowland primeval forest. Ecological studies in Białowieza Forest. *Geobotany*. Dordrecht, DR W. Junk Publishers.

Fartmann, T., B. Krämer, F. Stelzner and D. Poniatowski. 2012. Orthoptera as ecological indicators for succession in steppe grasslands. *Ecol. Indic.* 20:337–344.

Forup, M.L. and J. Memmott. 2005. The restoration of plant–pollinator interactions in hay meadows. *Restor. Ecol.* 13:265–274.

Forup, M.L., K.S.E. Henson, P.G. Craze and J. Memmott. 2007. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *J. Appl. Ecol.* 45:742–752.

Fitzpatrick, U., M.G. Murray, R.J. Paxton, J. Breen, D. Cotton, V. Santorum and M.J.F. Brown. 2007. Rarity and decline in bumblebees – a test of causes and correlates in the Irish fauna. *Biol. Conserv.* 136:185–194.

Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in measurment and comparison of species richness. *Ecol. Lett.* 4:379–391.

Goulson, D. 2006. The demise of the bumblebee in Britain. *Biologist* 53:294–299.

Griffin, S.R., B. Bruninga-Socolar, A. Morgan, M.A. Kerr, J. Gibbs and R. Winfree. 2016. Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. *Restor. Ecol.* 25(4):650–660.

Hopwood, J.L. 2008. The contribution of roadside grassland restorations to native bee conservation. *Biol. Conserv.* 141:2632–2640.

IPBES 2016. The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. S.G. Potts, V.L. Imperatriz-Fonseca, & H.T. Ngo (eds). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany, 827 pp.

Meyer, B., V. Gaebele and I.D. Steffan-Dewenter. 2007. Patch size and landscape effects on pollinators and seed set of the horseshoe vetch, *Hippocrepis comosa*, in an agricultural landscape of central Europe. *Entomologia Generalis* 30:73–185.

Michener, Ch.D. 2007. *The Bees of the World*. The Johns Hopkins University Press Baltimore.

Murray, T.E., M. Kuhlmann and S.G. Potts. 2009. Conservation ecology of bees: populations, species and communities. *Apidologie* 40:211–236.

Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Quaranta, M., Radchenko, V.G., Scheuchl, E., Smit, J., Straka, J., Terzo, M., Tomozii, B., Window, J. and Michez, D. 2014. *European Red List of Bees*. Publication Office of the European Union, Luxembourg.

Öckinger, E., A.K. Eriksson and H.G. Smith. 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biol. Conserv.* 133(3):291–300.

Ollerton, J. 2017. Pollinator diversity: distribution, ecological function, and conservation. *Annu. Rev. Ecol. Evol. Syst.* 48:353–376.

Pärtel, M., H. Bruun and M. Sammul. 2005. Biodiversity in temperate European grasslands: origin and Conservation. *Grassland Science in Europe* 10:1–14.

Potts, S.G., B Vulliamy, A. Dafni et al. 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101:103–112.

Potts, S.G., V. Imperatriz-Fonseca, H.T. Ngo, M.A. Aizen, J.C. Biesmeijer, T.D. Breeze, L.V. Dicks, L.A. Garibaldi, R. Hill, J.,

Settele and A.J. Vanbergen. 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540:220–229.

Prach, K. 2003. Spontaneous vegetation succession in central European man-made habitats: what information can be used in restoration practice? *Appl. Veg. Sci.* 6:125–129.

Pykälä, J, M. Luoto, R. Heikkinen and T. Kontula. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic .Appl. Ecol.* 6:25–33.

Pywell, R.F., E.A. Warman, L. Hulmes, S. Hulmes, P. Nuttall, T.H. Sparks, C.N.R. Critchley and A. Sherwood. 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.* 129:192–206.

R Core Team 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Söderström, B., B. Svensson, K. Vessby and A. Glimskär. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodivers. Conserv.* 10(11):1839–1863.

Steffan-Dewenter. I. and T. Tscharntke. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* 122:288–296.

Steffan-Dewenter, I. and T. Tscharntke. 2001. Succession of bee communities on fallows. *Ecography* 24:83–93.

Svensson, B., J. Lagerlöf and B.G. Svensson. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agricult. Ecosyst. Environ.* 77:247–255.

Taki, H., I. Okochi, K. Okabe, T. Inoue, H. Goto, et al. 2013. Succession influences wild bees in a temperate forest landscape: The value of early successional stages in naturally regenerated and planted forests. *PLoS ONE* 8(2):e56678.

Tarrant, S., J. Ollerton, M.L. Rahman, J. Tarrant and D. McCollin. 2013. Grassland restoration on landfill sites in the East Midlands, United Kingdom: an evaluation of floral resources and pollinating insects. *Restor. Ecol.* 21:560–568.

ter Braak, C.J.F. and P. Šmilauer. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows*: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY, USA.

Tscharntke, T., A.M. Klein, A. Kruess, I. Steffan-Dewenter and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8:857–874.

Williams, N.M. 2011. Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restor. Ecol.* 19:450–459.

Yamaura, Y., J.A. Royle, N. Shimada, S. Asanuma, T. Sato et al. 2012. Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. *Biodivers. Conserv.* 21:1365–1380.

Young, T.P. 2000. Restoration ecology and conservation biology. *Biol. Conserv.* 92:73–83.

Received January 3, 2018
Revised April 27, June 4, 2018
Accepted June 5, 2018

Supplementary material

Table S1. List of study sites, with information on vegetation structure and threats to xerothermic and sandy grasslands.

Table S2. List of species of Apiformes recorded in the 3 analysed landscape types.

The appendix may be downloaded from www.akademiai.com.